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THE CUTICULA AND SUBCUTICULA OF TRE- MATODES AND CESTODES

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THE membrane which forms the outer covering of the body of trematodes and cestodes and is usually called the cuticula differs in certain important particulars from that of other invertebrates, and its morphological significance has long been a matter of dispute. The most noticeable feature of this difference is the apparent lack of a hypodermis in these worms, the cuticula being bounded on its inner surface by the superficial muscle layers and the parenchyma which fills the body-cavity.

In the last few years, however, a theory of the cuticula, which in the early years of modern helminthology was the prevailing one, has been revived by Professor F. Blochmann (1896), who has presented its claims to recognition with so much force and ability that it has been accepted by most helminthologists and zoologists as best accounting for the facts. It has also found its way into some of the best text-books and bids fair to become, in the ordinary course of events, one of the dogmas of science.

According to this theory, the cuticula of trematodes and cestodes is a true cuticula morphologically, which is secreted by a hypodermis, as in other invertebrates. This hypodermis, however, has undergone a metamorphosis, for instead of forming a continuous layer of cells situated

immediately beneath the cuticula, it has dropped back of some or all of the superficial muscle layers into the parenchyma, its constituent cells have become more or less separated from one another, and it forms the broken or irregular tissue called the subcuticula.

Fig. 1, which is taken from Blochmann's paper and ap-

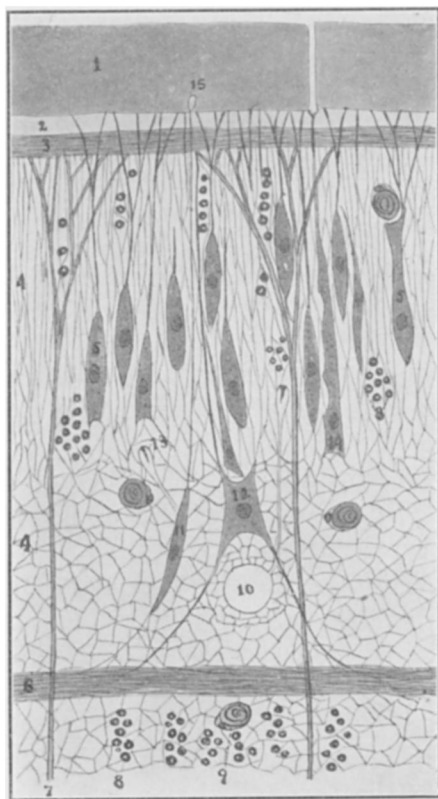


FIG. 1. Transverse section from Ligula, a cestode (after Blochmann). 1, cuticula; 2, basal membrane; 3, circular muscles; 4, parenchyma; 5, subcuticular cells; 6, nerve; 7, dorsoventral muscles; 8, longitudinal muscles; 9, calcareous body; 10, excretory canal; 11, sense-cell; 12, myoblast; 13, flame-cell; 14, gland-cell; 15, sense-organ.

pears also in Claus and Grobben's "*Lehrbuch*," Braun's "*Menschliche Parasiten*" and Lankester's "*Zoology*," represents a section of the body-wall of a cestode (Ligula) and shows the relation of the cuticula to the subcuticular

cells as conceived by Blochmann and adopted by the authors of these text-books.

Fig. 2 from Hein (1904), who follows Blochmann closely, shows the same relations in the digenetic trematodes. It will be seen in both these figures that the subcuticular cells form a distinct although irregular layer and are joined with the inner surface of the cuticula by long projections. These Blochmann and Hein regard as the ducts through which formative material is added to

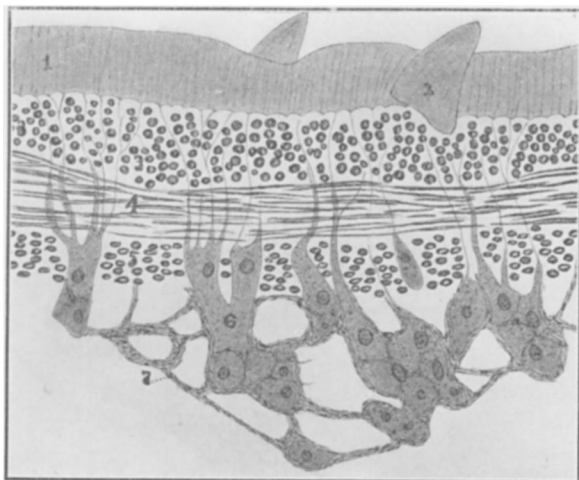


FIG. 2. Longitudinal section from *Fasciola hepatica*, a digenetic trematode (after Hein). 1, cuticula; 2, spine; 3, circular muscles; 4, longitudinal muscles; 5, oblique muscles; 6, subcuticular cells; 7, parenchyma.

the cuticula, of which these cells are thus the matrix. It will further be noticed in these figures that the subcuticular cells apparently do not form a part of the parenchyma in which they lie, and also that among them are sense cells and gland cells which are usually conceded to have an epithelial origin.

Another theory of the cuticula which is not very different from Blochmann's is that of Brandes (1892), who also considers the structure in question to be the product of the subcuticular cells (Fig. 3). These, however, he conceives to be single-celled glands which are joined with

the cuticula by means of ducts passing between the superficial muscle fibers. Brandes's theory is based upon an examination of a considerable number of monogenetic and digenetic trematodes, in both of which groups he finds practically identical structural conditions in the cuticular and subcuticular layers. His

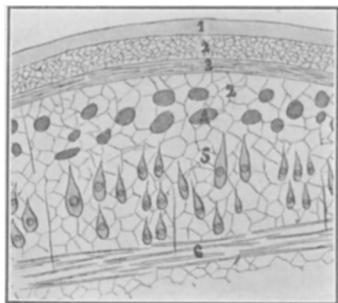


FIG. 3. Transverse section from *Onchocotyle appendiculata*, a monogenetic trematode (after Brandes). 1, cuticula; 2, parenchyma; 3, circular muscles; 4, longitudinal muscles; 5, subcuticular cells; 6, oblique muscles.

drawings, however, are very diagrammatic. The subcuticular cells certainly do not exist in any trematodes in the form in which he shows them, and those in his figures of monogenetic trematodes are not the subcuticular cells at all, but the single-celled glands which are present at the forward end of most of these worms.

Tennent (1906) and others have adopted Brandes's view.

It will at once be noted that the main difference between his theory and that of Blochmann lies in their interpretation of the subcuticular cells, the former holding them to constitute a hypodermis and to be consequently an epithelium of ectodermic origin, the latter considering them simple gland cells which are derivatives of the parenchyma.

These important theories, although they may seem to account for the facts in the animals investigated and to place the whole matter upon a substantial logical basis, have, however, met with considerable opposition, and, it seems to me, are not well grounded. It is quite evident that if they are true they must have universal application. If the subcuticular cells are the matrix of the cuticula, whether we consider them to be single-celled glands or the constituent parts of a hypodermis, then they must be present in all trematodes and cestodes, since this peculiar cuticula characterizes all of these worms (with the

exception of the Temnocephalidæ) from their early larval stages to those of the adult.

But this is far from being the case. The subcuticular cells are wanting in probably the whole group of monogenetic trematodes, also in most of the Aspidobothridæ and in certain other digenetic trematodes. Goto (1894, 1899) has made a careful anatomical study of over forty species of monogenetic trematodes belonging to some sixteen genera, and has found no subcuticular cells in any

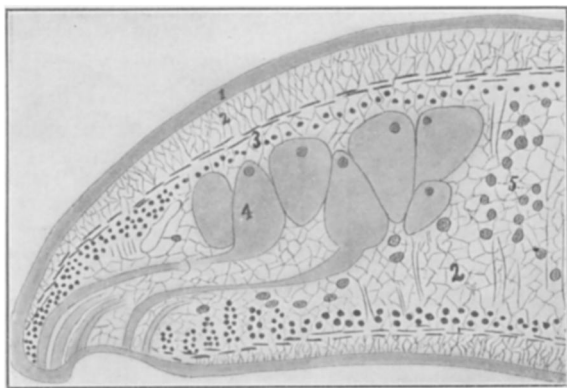


FIG. 4. Transverse section from *Dionchus agassizi*, a monogenetic trematode (after Goto). 1, cuticula; 2, parenchyma; 3, muscles; 4, single-celled glands; 5, parenchyma nuclei.

of them (Fig. 4). He directed his attention specially to the discovery of these cells in the worms studied by Brandes, but says:

Although I directed my special attention to the point, I have utterly failed to observe those subcuticular cells so beautifully drawn by Brandes in his figures in the very same genera that he describes.

Cerfontaine (1899) has also made a study of some twenty-eight species of monogenetic trematodes with the same result (Fig. 5).

It is true that peripheral single-celled glands are present in probably all of these worms, the ducts of which can be easily seen (Figs. 1 and 4) to pass not merely to but through the cuticula to the outside surface of the body. These gland cells are usually grouped at the forward end

of the body or in the neighborhood of the suckers, and are variously interpreted as sticky or mucous glands or as irritants to increase the flow of the juices which serve as the food of the worm. They do not extend over the whole body or any large part of it, and are not the subcuticular

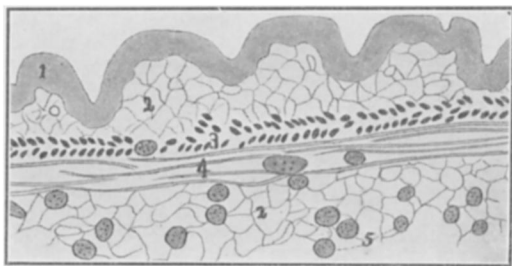


FIG. 5. Longitudinal section from *Squalonchocotyle vulgaris*, a monogenetic trematode (after Cerfontaine). 1, cuticula; 2, parenchyma; 3, circular muscles; 4, longitudinal muscles; 5, parenchyma nuclei.

cells, nor are they so considered by any authors who have studied them. They also differ markedly in shape from the subcuticular cells, being more or less pear-shaped and regular in outline, each cell having a distinct and single

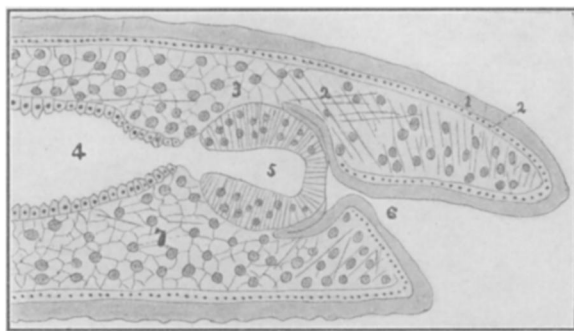


FIG. 6. Longitudinal section from *Stichocotyle nephropis*, an aspidobothrid (after Nickerson). 1, cuticula; 2, muscles; 3, parenchyma; 4, intestine; 5, pharynx; 6, mouth; 7, parenchyma nuclei.

duct of large size. The subcuticular cells, on the other hand, are often irregular in shape, often anastomosing with one another and in many cases having the appearance of parenchyma cells. They also show no ducts at all,

but in many forms are connected with the cuticula by branched or anastomosing processes (Figs. 1 and 2) which are interpreted by many to be ducts.

The lack of subcuticular cells in Aspidobothridæ has been shown by Monticelli (1892) and Nickerson (1902) for *Cotylogaster*, Nickerson (1894) for *Stichocotyle* (Fig. 6), and Osborn (1904) for *Cotylaspis*. Single-celled glands are, however, present in all these worms.

In the other digenetic trematodes and in cestodes, also, although subcuticular cells have been shown to be present in most of the forms whose finer structure is known, it is certain that some do not possess them. In *Distomum palliatum* and *Distomum reticulatum*, for instance, Looss (1885) found none of them, and in *Hemiurus crenatus* and *Gasterostomum gracilescens* Lander (1904) and Tennent (1906), respectively, found them only in very small numbers. In all digenetic trematodes and cestodes, also, it can very often be shown that the cells in question bear no adequate relation to the cuticula beneath which they lie. Thus they are present sometimes in certain parts of the body only, as has been shown in my study of *Apoblema* (1898), in which the appendix of the youthful distome, although covered with exactly the same cuticula as in the rest of the body, is entirely without subcuticular cells. The suckers, also, in cestodes and the tail of the cercaria have none of these cells, although they possess a cuticula.

In many digenetic trematodes, too, the subcuticular cells, although present, are entirely too few in number to produce the thick cuticula present, as shown in *Hemiurus crenatus* (Fig. 7) by Lander, and in numerous other cases. It must be remembered in this connection that the cuticula of trematodes and cestodes is probably at all times a growing tissue, which is constantly being renewed on its inner surface in proportion as it wears away on its outer, so that if the subcuticular cells are its matrix they should be equally present in all parts of the body and at all times of the animal's active life.

In many digenetic trematodes the cuticula is not of equal thickness on all parts of the body and these variations in thickness are not correlated with corresponding differences in the subcuticular cells beneath them. For instance, the cuticula of the appendiculate distomes has numerous transverse rings which give a longitudinal section a serrated appearance. These rings are due solely to

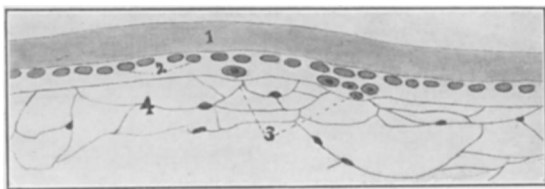


FIG. 7. Transverse section from *Hemimurus crenatus*, an appendiculate distome (after Lander). 1, cuticula; 2, longitudinal muscles; 3, subcuticular cells; 4, parenchyma.

variations in the thickness of the cuticula, the inner surface of it being quite smooth, and we might expect the subcuticular cells, if they secreted the cuticular, to be larger or more numerous beneath the rings. This is, however, not the case, these cells showing no variations whatever beneath these cuticular rings.

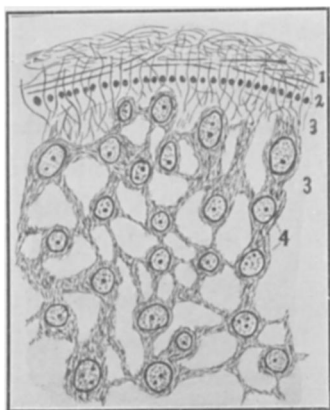
The relations of the spines, hooks, scales and other special cuticular structures to the subcuticular cells also furnish an argument against the epithelial or glandular nature of the latter. These spines and hooks are of very common occurrence and are often very prominent objects in trematodes and cestodes, their function usually being to aid in anchoring the parasite to its host. They are seen in their simplest form in the digenetic trematodes, (Fig. 2) in which they usually appear as specialized parts of the cuticula. In the monogenetic trematodes and the cestodes, on the other hand, they are often of huge size and of more or less complex structure and may extend beneath the cuticula among the muscles and the parenchyma cells.

That these organs are similar in essential structure and

in origin to the cuticula has been very well shown by Looss (1894), Young (1908) and other authors, who have traced their development and growth.

If now the cuticula is the product of the underlying subcuticular cells, we should expect to find some special development of them beneath the hooks and spines, especially where these are very large, just as in the integument of insects a cuticular hair or scale is invariably situated over the enlarged hypodermal cell which produces it. Nothing of the sort exists, however, in trematodes and cestodes. The subcuticular cells beneath the hooks and spines do not differ in size, number or arrangement from the adjacent cells, and in the monogenetic trematodes, which are often provided with gigantic hooks, no subcuticular cells at all are present. In the six-hooked embryo of cestodes the hooks make their appearance in the embryonic parenchyma, while there are as yet no subcuticular cells present. The parenchyma is thus the matrix of the hooks at this early stage of the animal's existence.

Another point of importance is the essential difference in structure between the cuticula of trematodes and cestodes and that of other worms and of arthropods in which the cuticula is the secretion of an undoubted hypodermis. In the former the characteristic lamellate structure of a



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FIG. 8. Section of wall of young cysticercus of *Tania serrata* (after Young). 1, cuticula; 2, muscles; 3, parenchyma; 4, parenchyma nuclei.

FIG. 9. Section of body wall of *Squalonchocotyle vulgaris*, a monogenetic trematode (after Cerfontaine). 1, cuticula; 2, nuclei in the cuticula; 3, parenchyma; 4, muscles.

typical arthropod or worm cuticula is never present (although it may be made up of several layers), but, on the other hand, a fundamentally fibrous structure can often be demonstrated with perfect clearness, the fibers being sometimes in very evident connection with the parenchyma beneath and a portion of it (Figs. 8 and 9).

In fact, the so-called ducts of the subcuticular cells are nothing more nor less than the fibrous projections of these cells which, together with similar projections of the parenchyma cells themselves, sometimes extend to, and occasionally, especially in young animals, into the cuticula. In certain cases these fibers may arrange themselves so as to form a series of vertical strands in the cuticula, passing between its inner and outer surfaces, and have been interpreted in the past to be pore-canals, structures which are probably not present in any trematodes or cestodes. Whatever toughness of texture the cuticula of these worms possesses is probably due to this fundamentally fibrous or leathery structure. The cuticula is further exceedingly elastic; it is often very soft or even semi-fluid and easily destroyed in caustic potash and as the result of maceration; and it is never moulted as a whole nor can it be usually separated from the tissues beneath—all of which characteristics are foreign to the cuticula of other worms and of arthropods.

The differences between an undoubted hypodermis and the subcuticular cells are also fundamental and very striking, and are not satisfactorily explained by Blochmann, who compares with them the hypodermal cells of *Hirudo* and other animals which may be more or less separated from one another by parenchyma and other tissues. The origin of these cells forms the embryonic parenchyma, as shown clearly by many authors, and the frequent anastomosing of them with one another and with the surrounding parenchyma, are characters which no hypodermis possesses.

It is true that there is a strong superficial resemblance between the subcuticular cells in cestodes—but seldom or

never in trematodes—and epithelial cells, without which it is not likely that any one would ever have thought of this epithelial theory. These cells in cestodes are, as we have seen, usually elongated and spindle-shaped and lie parallel to one another, so that they look a good deal like isolated epithelial cells. But it must also be noticed (Fig. 1) that all the other cellular elements of the peripheral region—the parenchyma cells, the gland cells and the sense cells—are also elongated and spindle-shaped and lie parallel to one another and to the subcuticular cells. Ap-



FIG. 10. Golgi section from a cestode (*Ligula*) showing the branched insertion of the dorsoventral muscles in the cuticula (after Zerneck). 1, cuticula; 2, the muscles; 3, sense-organ; 4, nerves; 5, sense-cell.

parently some common cause, in the nature of a tension in a dorsoventral direction, has acted upon the entire peripheral region of the body of the worm, distorting more or less all the structures in it. Leuckart (1886) has suggested—and Leuckart's suggestions are always fruitful—that this spindle form is due to the action of the powerful dorsoventral muscles which run across the

proglottid and are inserted in the cuticula of each surface by numerous branching strands (Fig. 10). He even thought that the spindle cells might be the tendons of these muscles, which, however, is not the case, since Zernicke (1895) and others have demonstrated the branched insertions just mentioned. It is my opinion, however, that it is the pull of these muscles and especially of their branched insertions which interweave themselves among all the peripheral tissues of the body (Fig. 10), which has thus distorted all the cellular elements in this region and caused them to assume their characteristic shape and appearance. And this opinion is confirmed by the fact that in the scolex and between the proglottids, where these muscles are weak or absent, the subcuticular cells are not spindle-shaped, but have the form of ordinary parenchyma cells (Leuckart).

The embryological and larval history of these worms also furnishes arguments against the epithelial theory. The cuticula comes into existence, both in trematodes and cestodes, before the subcuticular cells have differentiated and grows independently of them (Figs. 8 and 11). Its early growth has been well described by Looss for trematodes in *Diplo discus* (1892) and in a considerable number of distomes (1894) and by Roewer (1906) in distomes, and for cestodes by Young (1908) in *Cysticercus pisi-formis*. These authors show also very conclusively that when the subcuticular cells do finally make their appearance it is as differentiations of the embryonic parenchyma cells and that at no time is anything like an epithelium present in the position in which they are found (Fig. 8).

The moulting of the outer epithelium (ectoderm) in larval trematodes and cestodes has also an important bearing upon this question, inasmuch as in consequence of it the adult worm is entirely composed of tissues derived primarily from the interior embryonic cell mass (endoderm or mesenchyme). The subcuticular cells can not consequently be of ectodermal origin and can not be

homologous to the hypodermis of other invertebrates. In trematodes this moulting may occur in each of the larval stages. It has been directly observed in the miracidium many times, among others by both Thomas (1883) and Leuckart (1886) who saw the miracidium of *Fasciola hepatica* shed its ciliated ectoderm when it entered the liver of *Lymnæa trunculata*. In the redia and cercaria stages it has also been directly observed by a number of investigators. Looss has made the most complete record of his observations. He (1892, 1893, 1894, also Braun, 1893, p. 818) has seen both the redia and cercaria shed its outer epithelium in about a dozen species of distomes, as just remarked, after which procedure the young worm was covered with the definitive cuticula. This Looss considers the product of secretions of the entire body of the parenchyma.

Although the cercaria has thus been seen to shed its peripheral epithelium, there have been recorded a number of cases where it is not shed all at one time, portions remaining until the cercaria is fully grown or nearly so. The appendiculate distome I described some time ago (1898) was a good example of this procedure. The appendix of the young worm in this case retained its cercarian ectoderm although the male genital organs were mature and spermatozoa were being produced. The remainder of the body was without an epithelium, but was covered by the characteristic cuticula, which was also present beneath the epithelium on the appendix. This epithelium was soon after moulted and then the outer covering of the appendix was exactly similar to that of the rest of the body.

In cestodes the early stages of development are very similar to those of trematodes, the ectoderm having been observed by Schauinsland (1885), Leuckart (1886) and others to be moulted in exactly the same way. It is the opinion of many students of cestodes, however, that the stage in which an outer epithelium is present is passed over in most of these animals. The young worms thus

never have an outer epithelium, but the characteristic cuticula is their earliest body-covering.

Although there can be no doubt that the outer epithelium of trematode and cestode embryos and larvæ is often, perhaps usually, moulted, it must be mentioned that cases have also been recorded in which no such moulting has apparently taken place. Schauinsland (1883) has shown that in the embryo of *Distomum tereticolle*, the ectoderm gradually loses its cell boundaries and nuclei and becomes metamorphosed into a cuticula. A similar process has been described by Leuckart (1886) in the young redia of *Fasciola hepatica*, by Zeller (1872) in the embryo of *Polystoma*, and by other authors.



FIG. 11. Section of wall of a young cysticercus of *Tania serrata* (after Young). 1, cuticula; 2, parenchyma.

These facts and others which will be mentioned have led many helminthologists to subscribe to a third theory of the cuticula of trematodes and cestodes—that which sees in it a metamorphosed or cuticularized epithelium (ectoderm). This is one of the oldest of the theories relating to the cuticula, having been first proposed by Wagener in 1855, and in later years having such able supporters as Monticelli,

Goto, Nickerson and Braun, although the last named has apparently abandoned it in favor of Blochmann's theory. It is based mainly upon the facts that embryonic and larval ectoderms have been observed in a degenerate condition as just stated, and also that frequently nuclei are found imbedded in the adult cuticula. These nuclei are sometimes well formed (Fig. 12), but often have the appearance of being in a more or less broken-down condition and to be degenerating. Open spaces and vesicles are also often present in the cuticula.

Much has been observed which supports this theory. Braun (1893, p. 590) found numerous oval nuclei in the cuticula of *Monostomum mutabile*, Maclaren (1905) found

them in *Distomum* sp. (Fig. 12), Monticelli (1892, 1894) in a number of trematodes, Nickerson (1902) in *Cotyllogaster*, Cerfontaine (1899) in *Squalonchocotyle vulgaris* (Fig. 9): many other authors also have seen and described them. There can be no doubt that however one may interpret the alleged cuticularization of the embryonic and larval ectoderms,—and Brandes, Looss, Braun and others will not admit that it has been demonstrated,

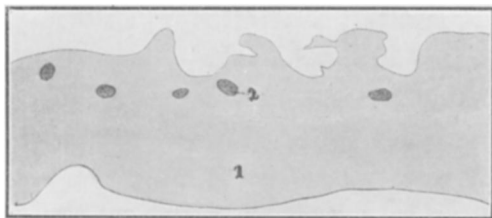


FIG. 12. Section of the cuticula of a distome containing nuclei (after Mac-laren). 1, cuticula; 2, nucleus imbedded in cuticula.

—nuclei or nuclei-like bodies occasionally appear in the cuticula of both larval and adult trematodes and cestodes. These have been variously interpreted by different authors. Blochmann (1896), for instance, asserts that they are the end organs of sense cells which are imbedded in the cuticula, while Looss (1893) thinks they may be portions of formed material in the act of passing from the parenchyma into the cuticula.

It seems to me that the occurrence of nuclei in the cuticula has been recorded by too many competent observers to be explained away in any such manner. They undoubtedly do occasionally occur, being either nuclei which are parts of a degenerating epithelium or perhaps those which belong to the peripheral portion of the parenchyma and have become enclosed in the rapidly forming and growing cuticula. This last probability is strengthened by the observation of Maclaren (1905) and others that such nuclei occur most frequently in the cuticula of young worms, and by those of Young (1908) and Cerfontaine (1899) who show, respectively, that the cuticula

of the very young larva is composed essentially of fibers and nuclei closely bound together (Fig. 11) and that the adult cuticula may be in direct connection with the subjacent parenchyma and contain some of its nuclei (Fig. 9). It is conceivable, however, notwithstanding these facts, that foreign objects such as particles of coagulated blood, which often adheres to the outer surface of these worms, could be forced into the soft cuticula from the outside as a result of the pressure to which the worms are often subjected in their natural environment, or perhaps in the compressor or under the cover-glass of the investigator, and thus appear like degenerating nuclei in it. The vesicles, which often appear in the cuticle, are probably artefacts due to the influence of reagents on the soft cuticula of a dying or a compressed animal. The cuticula also macerates very rapidly, in fact it is often the first part of the body to show death-changes, and may easily become vesicular by the passage of fluids or gases into it from the parenchyma or from the outside.

In my own opinion this theory of the metamorphosed epithelium breaks down, at least as a universal theory, for several reasons. In the first place, the outer epithelium is undoubtedly moulted in very many larval trematodes, as has been observed by many competent observers, and a worm can not both shed its epithelium and still enjoy the possession of it, even in a modified form. The theory can not thus have general application. In the second place, even if the ectoderm of the embryo or larva is cuticularized in certain cases, as has been observed, the cuticula of the adult worm is not yet accounted for, as the worm increases in size many-fold, often many thousand-fold, while growing from the larval to the adult condition. In other words, the cuticula of the mature worm may be quite a different structure from that of the larva, and if it is true that the cuticula of the larva is a metamorphosed epithelium, then that of the adult is formed of a different material and in a different way. Inasmuch as the cuticula is constantly growing on its inner

surface and being flaked off on its outer, it is not a structure which is formed once for all but one which depends on a more or less uniform secretion from the tissues beneath.

What then is the morphological significance of the cuticula of trematodes and cestodes if it is neither a metamorphosed epithelium nor the product of an underlying hypodermis or of single-celled glands. I believe that it is the peripheral portion of the parenchyma which forms the outer coating of the body after the disappearance of the larval epithelium (ectoderm), and which has been solidified into a thick membrane by the secretion of cuticular substance from the whole body of the parenchyma. That the entire parenchyma can thus have a secretory function is proved by the formation by it of the fluid with which it is permeated and its vesicles are filled and also of that which fills the cavity of a cysticercus.

This theory seems to have originated with Leuckart (1886, p. 367). It has been explained and defended at great length by Looss (1893, 1894, also Braun 1893, p. 818, note) and subscribed to by Pratt (1898), Cerfontaine (1899) and Young (1908). It is in certain respects an unusual theory, inasmuch as it implies the absence of an integumental covering of ectodermic origin, which is characteristic of the rest of the Metazoa. But the life conditions of trematodes and cestodes are peculiar and unusual. These worms are exclusively parasitic animals, being the only large groups of Metazoa, so far as I recall, of which this is the case, and this parasitic habit is undoubtedly correlated with the disappearance of the larval ectoderm and the formation of the parenchymatous cuticula, as well as other special features of the structure of these worms.

The most primitive trematodes, the *Temnocephalidæ*, are an exception to the rest of the group in possessing an integument composed of a cuticula with an underlying hypodermis, although having the typical trematode structure in other respects. These animals are found adhering

to the surface of turtles and fresh-water crustaceans and are not true parasites, inasmuch as they feed upon small animals in the water and not upon the vital juices of the host. They probably form a connecting link between turbellarians and trematodes, representing the first step of the ancestors of the latter towards the acquisition of parasitic habits. The next step was taken as the result of the migration of the worms from the surface into the mouth and cloaca and on to the gills, and then into the internal organs, of the aquatic hosts. The worms thus became true parasites. They learned to feed upon the blood or the other juices of the host and were habitually enclosed or immersed in its tissues and exposed to the disintegrating action of its fluids. It is probable, as a result of these things, that the changes occurred which characterize the body-covering of these worms. The integument which is common to most worms apparently would not furnish a sufficient protection to animals thus situated, and it consequently came about in the course of their evolution that the outer epithelium with its cuticula was moulted or at least disappeared and the parenchyma acquired the property of forming a thick cuticula-like membrane on its outer surface to protect the animals from the peculiar dangers of their environment. A protective function similar to this is, as Leuckart points out, very frequently exercised by cuticula-like connective tissue structures of various kinds throughout the animal kingdom.

Von Graff (1903) has made the observation, it is interesting to note, that in certain of the parasitic turbellarians (*Syncoelidium*) a process similar to this has evidently gone on, for the animals have lost their integumental epithelium together with its cilia and are covered with a cuticula similar to that of trematodes.

The first steps in the formation of the cuticula have been minutely observed, as already stated, in the trematodes by Looss (1892, 1903) and Roewer (1906) and in cestodes by Young (1908). According to Looss, it first

appears as a fine line between the muscle-layers and the outer epithelium (ectoderm) of the redia and cercaria, which gradually broadens and when the epithelium is finally shed, becomes the outer covering of the body. Looss has observed this proceeding in a dozen or more different species of trematodes and believes it to be general to the entire group.

According to Young, the cuticula of the young cysticercus is a delicate layer which is composed of a groundwork formed of fibrillar projections of the embryonic parenchyma cells and a homogeneous translucent cement-like substance produced by these cells (Figs. 8 and 11). The subcuticular cells have not yet differentiated from the embryonic parenchyma. The young cuticula soon begin to scale off on the outer surface and is constantly being added to on the inner. In the course of time two layers show themselves in the cuticula, the inner of which alone contains the cement-like substance, the outer layer, which in later stages may be very thin or be entirely lost, forming the so-called hair-layer which sometimes characterizes the outer surface of cestodes and is exclusively fibrillar.

The later history of the cuticula is a continuation of its larval history. Although formed principally as a secretion of the parenchyma, it is at all times a part of it and will often show, even in the adult stage, a fundamentally fibrillar structure. It is also, as has been stated, never moulted and can not be easily separated from the structures beneath.

Very important in a study of the whole question, is the relation of the gonoducts and the excretory vesicle to the surrounding parenchyma, inasmuch as the walls of these structures have essentially the same structure as the outer body-wall, being lined by a cuticula at the back of which are the parenchyma and usually muscle fibers. What then is the developmental history of these ducts? It has recently been shown by Balss (1908) in cestodes and Roewer (1906) in trematodes that the history of the

formation of the gonoducts as well as their structure, is essentially similar to that of the body-wall. The walls of each of these ducts (except those of the uterus in cestodes) are formed at first of a single-layered epithelium which develops from a primitive chord of epithelial cells by the appearance in it of a lumen. This epithelium, however, quickly degenerates and disappears and at the same time the surrounding parenchyma secretes a cuticula which forms the permanent coating of the tubes. The spines which are often present in the cirrus and vagina are formed in the same way.

The terminal excretory vesicle has also primitively an epithelial wall like that of the gonoducts, as has been shown by Looss (1894) and in my study of *Apobolema* (1898), which is replaced by a parenchymatous cuticula as in the case of the gonoducts.

The cause of the change in the structure of the walls of these ducts from an epithelium to a parenchymatous cuticula is probably identical with that which has been brought about a similar change in the structure of the body-wall. Not only is the outer covering of the animal apt to be affected injuriously by the juices of the host, but the walls of the large ducts opening to the outside as well, and both have consequently undergone an identical transformation.

What then are the origin and function of the subcuticular cells? That they belong genetically to the parenchyma has been proved with the utmost conclusiveness by the embryological researches of Looss, Young, Balss and others. The conclusion, based by Blochmann and Hein upon anatomical evidence, that they form an epithelium needs, but has not yet received, embryological support; in fact, not a scintilla of embryological evidence has been produced either by them or any one else in the thirteen years which have elapsed since Blochmann's paper was published. And purely anatomical evidence in an obscure matter like this should be received with the greatest caution, especially since the extreme parasitism of these

worms has affected all their organs and tissues in so marked a degree.

The function of these cells is a much more difficult matter to determine, and two diametrically opposed classes of views have been expressed concerning it. According to one of these, they form a specialized tissue with either a secretory or an absorptive function. According to the other, they are an unspecialized embryonic tissue, which has no direct physiological relation to the other structures of the body.

If the almost unanimous decision of all the investigators who have studied trematodes and cestodes is to be accepted, the subcuticular cells are glandular or secretory in function and, as we have seen, the cuticula is the product of their secretion. Some years ago (1898) I suggested that they (as well as the single-celled glands) may secrete, not the cuticula itself, but some substance which tends to render the cuticula immune to the disintegrating effects of the body-fluids of the host in which they pass their lives. That the cuticula of endoparasitic trematodes and of cestodes does possess some special means of protecting itself and the other tissues of the worms seems certain. Looss, for instance, has taken *Distomum tereticolle* from the stomach of the pike, where the worm was pressed tightly against the stomach-wall by large masses of actively digesting food. Something in this case must have prevented the worm from being digested, too. This special means of defense is not to be looked for in the physical structure of the cuticula itself, which is usually soft and easily injured, but in some chemical substance which neutralizes the action of the juices of the host. It is possible that the subcuticular cells secrete some such substance, especially as the ectoparasitic trematodes, which are in most cases either not surrounded by the tissues of the host or are only partially so, do not, as we have seen, possess these cells.

What the reaction of these secretions would be must depend upon the nature of the fluid in which the worm is

immersed. If it lives in the stomach of the host, for instance, the reaction would probably be alkaline and the action of the digestive juices would thus be neutralized. In other locations the reaction would be different and might be very complex.

A small minority of investigators, however, but important and influential though small, does not believe in the glandular function of the subcuticular cells. Rindfleisch and Leuckart (1886, p. 366) first expressed the opinion that, in cestodes at least, they are simply peculiarly formed connective tissue cells which in certain places may lose their spindle form and assume quite the form of ordinary parenchyma cells. This is the case, for instance, as already stated, in the scolex and between the proglottids.

Looss (1893) also regards the subcuticular cells as connective tissue structures, interpreting them as embryonic and unspecialized cells which are destined to develop into parenchyma and muscle strands as the worm increases in size, and he supports his views with such a mass of detailed observations and such cogent reasoning that it is likely they would be generally adopted if the belief in the secretory nature of the subcuticular cells were not so firmly fixed in the literature of the times.

Looss shows that the interior cells of the germ-balls of the cercaria develop into the nervous system, the genital organs, the intestinal cœca and the parenchyma—all after the first appearance of the cuticula. But all of these cells do not at once so develop. The young worm must grow often many thousandfold before it reaches adult size, and this increase in size is made possible through the persistence in an undifferentiated condition of certain of these interior embryonic cells, which during the life and growth of the worm are constantly forming new parenchyma cells, as well as other structures. The formed parenchyma cells do not divide. In the cercarian tail, which is destined to have but a very short existence, all of these cellular elements become parenchyma cells and

muscle strands and no embryonic cells persist; hence no subcuticular cells are present.

Originally these indifferent cells lie around all of the growing organs, especially the genital organs, as well as near the periphery of the body. But in the course of the growth of the worm all disappear except those near the periphery, which become the subcuticular cells and may remain throughout life, giving rise to new parenchyma cells, and also to muscle strands and to flame-cells. In old digenetic trematodes, however, they may also disappear (Lander, Maclaren). Looss compares these cells to the cambium of plants, which is also an indifferent tissue which gives rise to certain specialized tissues throughout the life of the plant.

The only authors who have fully subscribed to this theory, so far as I know, are Nickerson (1894) and Stafford (1896), who support it by observations drawn from the study of *Sichocotyle* and *Aspidogaster*, respectively, although Schuberg (1894), Lander (1904), Balss (1908), Young (1908) and others have declared in favor of the parenchymatous origin of the subcuticular cells.

That so few have done so is probably due, as I have already indicated, to the fact that the belief in the glandular nature of the cells in question is so firmly fixed in the minds of helminthologists as to have axiomatic force. But it must never be forgotten, notwithstanding this circumstance, that this particular function has never been proven for these cells. No one has yet seen them produce a secretion and the supposed ducts that are seen in connection with them in some, although by no means in all species, and the possession of which is perhaps the principal proof which has been brought of their glandular nature, are not ducts at all. In contrast to them we might indeed place the single-celled glands, whose ducts are always perfectly plain and whose secretion can be seen. It must also be remembered that neither Leuckart nor Looss, each of whom, it will be generally conceded, has surpassed all contemporary investigators in his knowl-

edge of parasitic worms, has attributed a glandular function to these cells, but, as we have seen, has interpreted them in quite a different way.

SUMMARY

1. The cuticula of trematodes and cestodes is not homologous to that of other worms and of arthropods.

2. The cuticula of trematodes and cestodes is the peripheral portion of the parenchyma, being composed mainly of secretions of it.

3. The subcuticula is not an epithelium or a hypodermis, but belongs genetically to the parenchyma.

4. The subcuticular cells are not present in the monogenetic trematodes, in most of the Aspidobothridæ and in many digenetic trematodes, or in any trematodes or cestodes during the earliest larval stages when the cuticula first forms.

5. The function of these cells is not known, and although most authors have ascribed a glandular or secretory function to them it seems likely that they form an indifferent, embryonic tissue which develops into specialized tissues as the worm increases in size.

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